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INVESTIGATION INTO THE EDGE EFFECT BY USE OF CAPTURE-RECAPTURE DATA IN A VOLE POPULATION[1]

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INTRODUCTION

Recently, as the progress in study of secondary productivity with small mammals, we have come to be confronted with the problem of how to convert estimated populations into densities. The question is, in effect, how to deal with the phenomenon, called "edge effect", which is induced explicitly by the fact that a limited-sized, sampling (trapping) quadrat is laid in a part of a population-covered area.

The phenomenon is conceived to have much to do with the following two agents; it is natural that the traps on and near the edge of a quadrat should bear higher probability than do those in inner square to be visited either (1) by animals settling in the adjoining area outside the quadrat or (2) by those immigrating from a distance. It seems to be a current explanation that the edge effect such as perceived from undue enhancement of catch per trap (station) at the edge part can be due to both agents. To say nothing of the effect of invasion, no strict theoretical analysis of the effect of adjoining outside settlers upon the increased edge catch has ever been attempted to test if the above interpretation is entirely justifiable.

DICE (1938) put forward the wellknown idea of additional boundary strip to calculate densities from estimated populations making allowance for mean sizes of home range. His theory, pertinent only to the first agent of edge effects, has never been refuted by anybody so far as I know. Nevertheless, many students are seeking to find intra-plot assessment lines demarcating such an inner square as free from edge effects.

Although the edge effect can superficially be checked up from catch per trap gathered by removal methods, the capture-recapture method is desirable to make a careful inquiry into the phenomenon, supposing that the first agent plays an important role. For the aim, it is required to know natural range sizes and the way of range shift and migration.

The present work was planned to explicate actual aspect of the edge effect on the basis of caputre-recapture data taken in two similar plots during a period only 12 days long, but check of traps was made twice a day and the study population, consisting almost entirely of a single species, of rather high density (60 or so per

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acre). Thus no small amount of helpful information could be available.

STUDY PLAN AND METHODS

The field work was conducted from 8 through 19 August, 1970 on two plots (A, B), laid about 200 m apart from each other in the grassland within the enclosure of Sugadaira Biological Laboratory, Nagano Pref. The objective vole (*Microtus montebelli*) is exclusively predominant among the small mammal community in this highland region. Capture-recapture works of the populations on the study plots had been carried out at successive intervals for the research of population dynamics of the vole since 1966 onward (KANAMORI and TANAKA 1968).

The scheme of the present work common to both plots was as follows:

Series	(1)	(2)	(3)
Date (Aug. 1970)	8~11	12~15	16~19
Trapping area	Whole area (100×100m)	Inner square (60×60m)	Inner square (60×60m)
Trap spacing (*d*)	10m	10m	5m

Three series, each equiped with diverse designs as shown above, of the work were sequentially executed. The whole area could be divided into the external belt and the inner square by demarcating dashed lines, as illustrated in Figs. 1~3. The external belt was removed after the last check of Ser. (1) finished. The trapping area was covered by a grid formed of single-catch live-traps, each of which was, accompanied with a metal shelter-cover, set on respective stations spaced a given distance (*d*) apart. Check of traps was made twice daily, in the morning and in the evening, in every series. No prebaiting was performed in any cases.

By way of convenience, individual growth stages were distinguished from each other according to body weight as in the following:

Juvenile (15g or less), Subadult (16~19g), Adult (20g or more)

APPROACH BY HOME RANGE ANALYSIS

Just now I remarked that knowledge of the natural size and the real way of shift of home ranges is first of all needful for interpreting rightly the facts underlying the edge effect. The scheme of this work was projected along the very line.

Numbers of papers aiming at home ranges have thus far been published by many ecologists of small rodents. It is no exaggeration to say, however, that we can not yet just be certain if we reach the truth of home range even in case we adopt an up-to-date method. For many reasons, the research of home ranges is at a standstill; one of those might be the prevalence of theoretical studies, which seem to stand on idealism rather than on substantialism, among researchers (TANAKA 1963).

Trapping has long been in common use for range study because of its advantage in supplying us with range data of many animals simultaneously with sampling for census during a given period; but yet nobody could affirm outright that a trap-revealed range, *per se*, always indicates the truth, if he is acquainted with methodological difficulties, pertaining to trapping procedure, which are referable to the question of trap-response on the part of animals (TANAKA 1956, 1961, 1963, KANAMORI and TANAKA 1968).

By way of compensation for the difficulties, several current methods using telemeters, isotopes, smoked paper and so on are now in process of development. Of these, the isotope method is accounted as best in practical utility for voles, yet it has a drawback in supplying us with range data of only a few animals at a sacrifice of heavy labor in the course of work. Its another disadvantage is the fear that animals are disturbed in natural behavior by surveyors with GEIGER counters making round of study areas.

Not all the data of trap-revealed ranges are unreliable. We (TANAKA 1961, KANAMORI and TANAKA 1968) have as yet maintained in the light of field evidence that the observed range length (STICKEL 1954, abbreviated to ORL in the text ensuing) serves as a just measure of natural range sizes. In this study, I try to approach the natural size and shape of home ranges by the help of ORL and another related measure ORW (observed range width) as well.

ORW is defined as maximum distance between capture sites measured in the direction perpendicular to ORL. Then ORL and ORW correspond to the long and the short axis of an elliptic home range respectively. The notion that an elongate rather than circular shape reflects universality in real range pattern was first proposed by MOHR (1965). Later, MAZURKIEWICZ (1969, 1971) offered elliptical modification of the home range pattern, determined conforming to bivariate normal distribution, on the same empirical basis as that MOHR stood on. As a result of analysis of range data in the vole population, I could substantiate that there is a prevailing tendency for home ranges to be elliptic in shape. But it has been verified that one had better never depend on the normal distribution to calculate lengths of long and short axes of elliptic ranges; the demonstration for that will be presented later on.

A configuration of trap-revealed range for each vole, unless it showed any range shift during the period under observation, was formed by circumscribing the entire assemblage of capture loci (excluding occasional sallies as defined by BURT 1943) of one and the same individual that was captured six times or more, thereby the resulting contour leading to a polygon. At present, we usually prefer to take a polygon than consider an ameboid outline as natural range shape notwithstanding the idea of BURT (1943).

When a range shift occurred to a vole, separate range outlines alloted respectively to before and after the shift were provided (these separate ranges were connected with arrows or concave lines) in the figures (Figs. 1, 2, 3). A geometric center of activity (GCA), which was determined from an assemblage of capture loci within each range outline, hence two or more GCAs being given to a vole that indicated

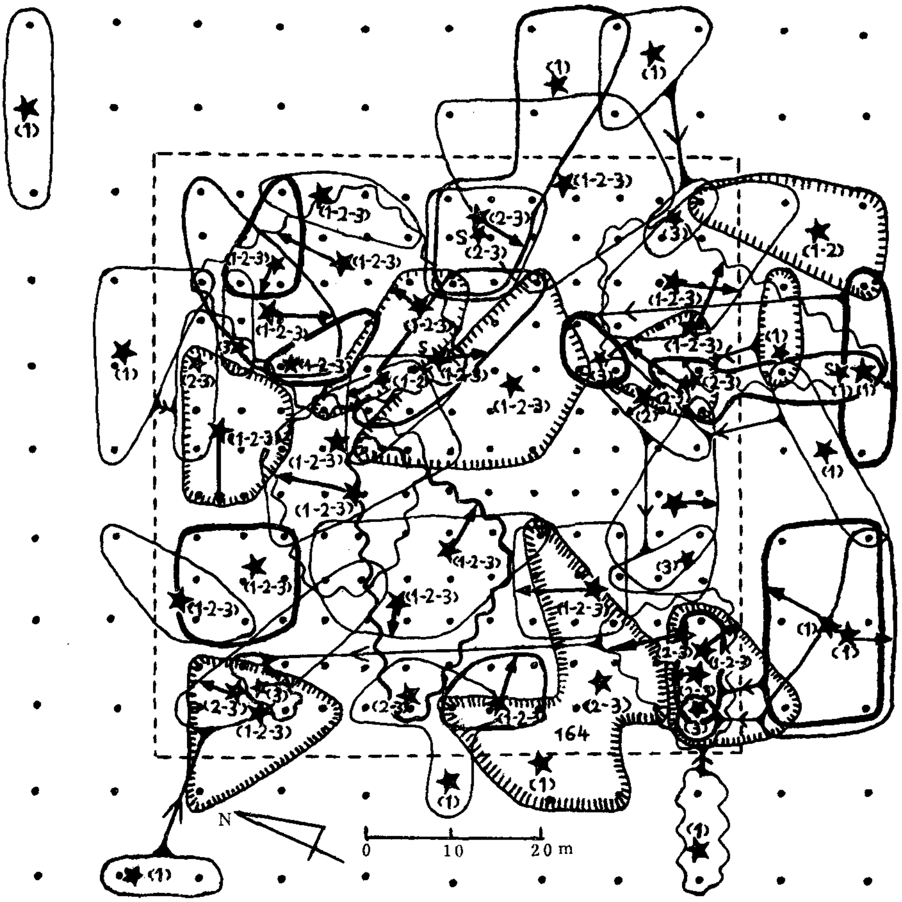

Fig. 1. Map of home range configurations for females, captured 6 times or more, in Plot A :dots stand for trap sites (stations), inner square sites being delimited by dashed lines; pentagrams for GCA (geometric center of activity); figures in parentheses attached to GCA for series nos.; typed figures within or near particular range contours for individual nos.; J (juvenile) or S (subadult) on GCA for growth stage at the time a vole appeared at first in this work, but no signs of "adult" being marked down.

range shift, was by way of reference denoted at its approximate locality in the figures.

By the way, I would like to touch territoriality ; any trend of it is seldom noted, seeing how much individual ranges are overlapping with each other in adult females (Fig. 1) as well as in adult males (Figs. 2, 3).

As stated by STICKEL (1954), there seems to be no completely objective method of distinguishing sallies from normal range travels. But, although a few voles of the sample were recognized to have traveled abruptly outside the home range by somewhat subjective judgement, if one hesitates to remove such sally records for fear of introducing personal bias, he should lead to be more seriously biased in estimating natural range sizes on an average.

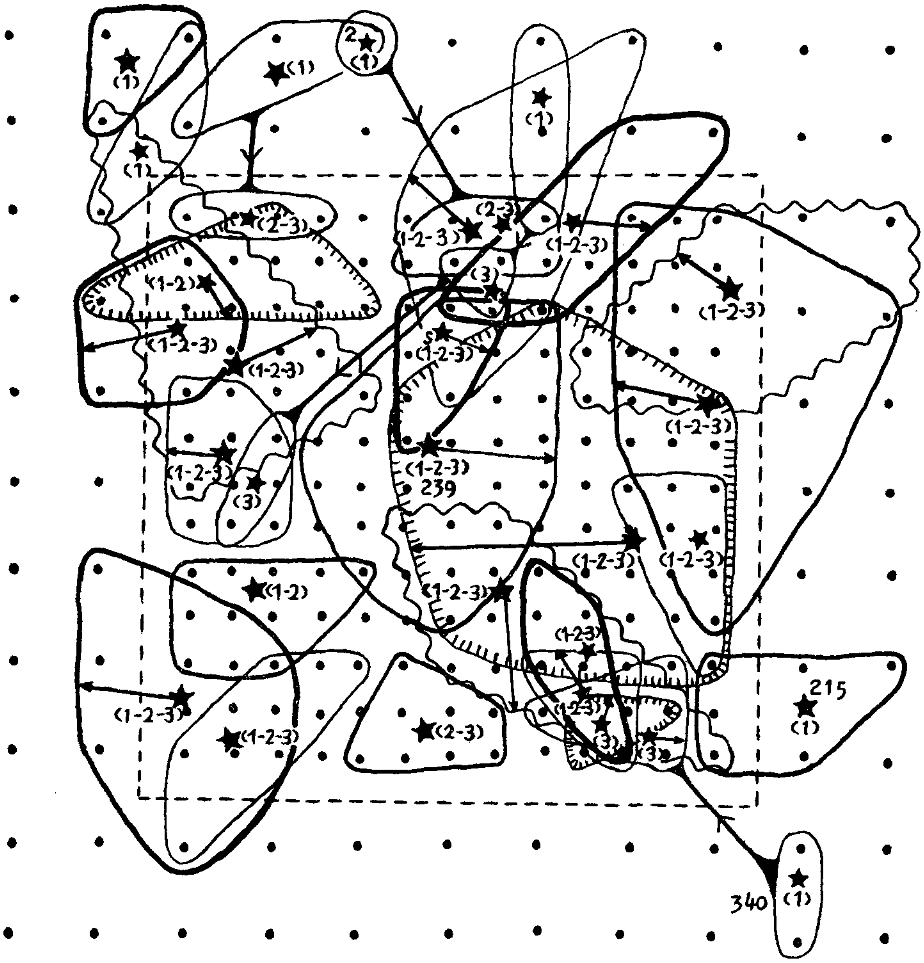

Fig. 2. Map of home range configurations for a part of male group, captured 6 times or more, in Plot A: small figures on GCA stand for number of capture times at one trap; other symbolism as in Fig. 1.

As for range shifts, we are usually cautioned not to examine an animal's movement too a long while so as to exclude shifts from normal range travels. But, within the extent of normal travels, a trap-revealed range grows larger incleasingly with rise of capture times of an animal until it is leveled off. Some authors consider the stable, reliable range size to be obtained after 10 times of capture, but there is yet no unified valid notion about it.

Through our studies (TANAKA 1961, KANAMORI and TANAKA 1968), it has been proved that such range sizes as leveled off approximately are given after 5 or 6 times of capture with Japanese voles. MAZURKIEWICZ (1971) evidenced, from the viewpoint of standard errors in range size, that 5 or more times capture can be accepted as qualifying specimens for collective analysis in a vole population. Conse-

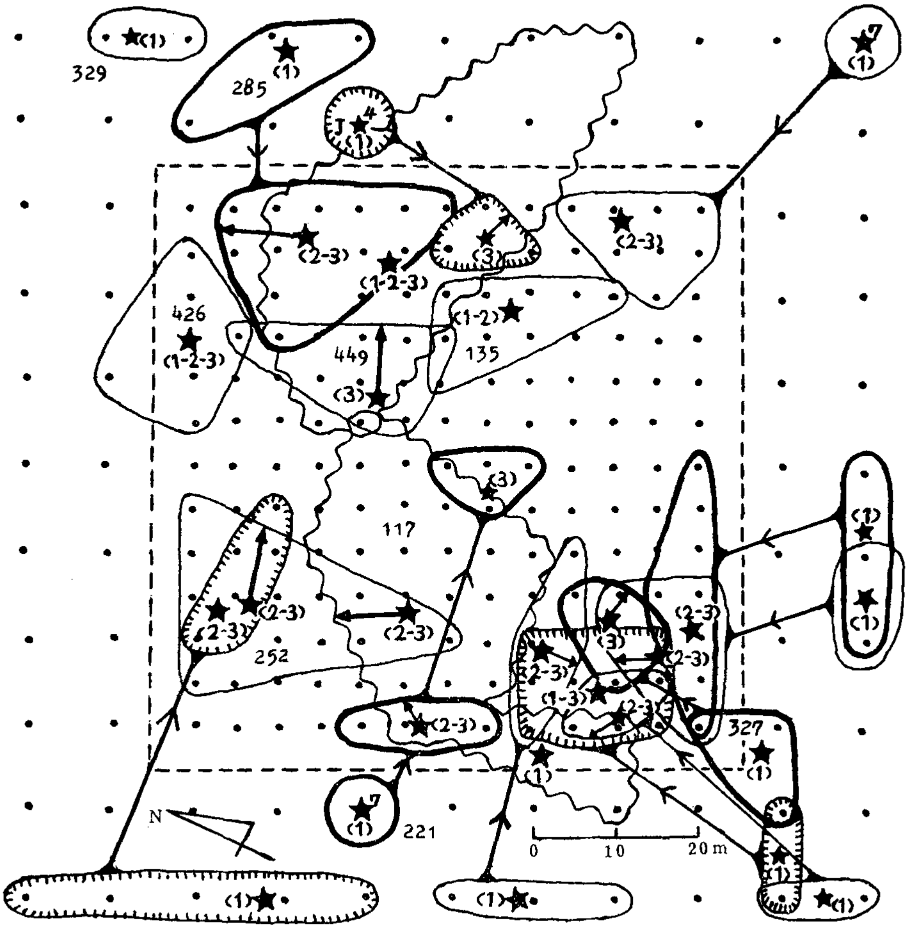

Fig. 3. Map of home range configurations for the rest of male group, captured 6 times or more, in Plot A: symbolism as in Figs. 1 and 2.

quently, it is just for me to have resolved that voles captured 6 times or more are qualified for range study. Such specimens provided me with considerable information about their home range.

Location, conservation and shift of home ranges were inspected by the analysis of range configurations on the maps (Figs. 1~3). Every range contour, given to each animal, through three series of the work, contains all the capture loci occurred to each and cruising lines connected between these successive loci. As a result, diverse patterns in animal behavior pertaining to its home range were discerned. On the supposition that only the inner squares of the plots were the proper census areas, the variations could be grouped into eight types, even though some of them graded into each other.

a. *Ingress range-shift*

Range was on the external belt (EB) in Ser. (1) but on the inner square (IS) in both Sers. (2) and (3) or in only (3), occasionally shift occurring in (2) and (3) (ex.: No. 340, Fig. 2; Nos. 285, 221, Fig. 3).

b. *Partial-ingress range-shift*

In Ser. (1), range streched to a large extent on EB but reached to one capture site of IS or it extended from the edge of IS to EB, while, in the later series (2) and (3) or in only (3), it streched more or less extensively within IS (ex.: No. 164, Fig. 1; Nos. 327, 117, Fig. 3).

c. *Range-conservativeness*

Range was kept at nearly the same location over all the series; i. e. it extended on IS or from IS to EB in Ser. (1), and every range (or its part) of the same vole localized on IS in different series could actually or probably be, to a consierable degree, superimposed on each other (ex.: No. 239, Fig. 2; No. 426, Fig. 3).

c′. *Quasi range-conservativeness*

Range clearly shifted from the place in Sers. (1) and (2) to that in (3), other things being the same as in Type c (only one case of the sample, not shown in Figs.)

d. *Uncertain ingress range-shift*

Range never appeared in Ser. (1) but did in both (2) and (3) or in only (3); i. e. this type is uncertain as to whether or not immigration occurred during the period (2) and (3) on account of the fact that no capture happened in Ser. (1) might have not always been traced to absence of a vole from anywhere in the plot (ex.: Nos. 252, 449, Fig. 3).

e. *Uncertain egress range-shift*

Range was located in both EB and IS or on IS only in Sers. (1) and (2) or in Ser. (1) only; i. e. this type also is uncertain as to whether or not emigration occurred in either Ser. (2) or (3) on the same account as in Type d (ex.: No. 215, Fig. 2; No. 135, Fig. 3).

f. *Outsider*

Range never appeared anywhere in the plot except that it did exclusively on EB in Ser. (1) alone; i. e. this type must probably have not been concerned with censusing in the proper area (IS) (ex.: No. 329, Fig. 3).

g. *Vagrant*

Capture happened in all the series or in the first and last series, and the overall range through these series streched very large distance, whereas it looked as if the concerned vole failed to settle a home range, even if it had occasionally a local small range (no example shown in Figs.)

Frequency distribution of these patterns is exhibited in Table 1. The sample consisted of the voles which were captured 6 to 26 times. It seems to be allowed to think that such a sample may represent the population, other than extremely ephemeral animals, which was present on some terrain covering the plot area and the adjoining outside area during the study period.

Table 1. Frequency distribution in range-behavioral patterns among the sample of specimens that were captured 6 times or more.

Types	Plot A		Plot B		Total
	Female	Male	Female	Male	
a	8	12*	4	13	37(20.2)
b	5	4	2	3	14(7.7)
c	23	18	25	29*	95(51.9)
c′	0	0	0	1	1(0.5)
d	2	4	2	5	13(7.1)
e	2	4	3	4	13(7.1)
f	1	3	2	1	7(3.8)
g	2	0	0	1	3(1.6)
Total	43	45	38	57	183(100.0)

* One vole of the stared groups each was juvenile at the first catch in Ser. (1), but all others of the sample were adult or supposed to have grown to adult at latest in Ser. (3).

From the table we can admit, first, that Type c for conservativeness possessed the majority (52%), and, second, that both types a and b combined (holding 28%) occurred in appreciably high frequency contrary to our anticipation, for we have something like a common notion that a capture-recapture trapping in itself causes, if any, no important amount of invasion by outside residents onto a census area. But lately some Polish ecologists are warning us that too long a prebaiting may induce considerable invasion.

STICKEL and WARBACH (1960) tried grouping range behaviors of the deer mouse in like manner as I did in one respect but in very different ways in another (they traced maps and shifts of home range as long as 5 years), so their and my findings are not rightly comparable with each other. Of their four patterns, "stable ranges", just equivalent to my type c, possessed the greater majority (79%) of their sample, too, whereas nothing equivalent to my ingress types (a and b) has been found out. The reason for the last fact is probably that they could not help confining theirselves to remarking intra-plot behaviors of animals under the circumstances of their study.

Among the eight patterns in Table 1, the three (a, b, c) look most likely to be immediately related to the question of edge effect, while the rest look much less important in view of either their qualities or their frequency rates; but it is interesting that the uncertain types of both egress and ingress was equal to each other in the frequency rate.

Supposing the inner square to be the proper census area as noted at first, we are assured that all the voles of Type c were sedentary ones at least for the census period of Sers. (2) and (3), and that some voles of Type d were also such. These residents are theoretically qualified as typical objectives of censusing, but in fact we are unwillingly led to treat transients or vagrants together with residents in usual censuses, since we cannot easily discriminate the unqualified from the qualified ones.

Home ranges of the resident voles are each localized in the proper census area, some of them, however, extending over its border lines (outermost trap rows). According to the rule of Dice (1938), every individual whose range center[1] is located inside the additional boundary strip line (dashed line in Fig. 5; I shall call it "Dice's assessment line" henceforth) should be considered to be included in the calculation of densities.

As described later on, the additional strip width could be given at 9.2 m, which is nearly as wide as trap spacing in EB. Therefore it has turned out that not only the resident voles, localized on the border line, but also the voles of Type b (partial ingress) and some voles of Type a (complete ingress) whose range in Ser. (1) streched from the outermost to the second inner trap rows of EB, ought to be included in the density count. Hence the rest of Type a whose range covered exclusively the outermost trap rows (of EB) in Ser. (1) should be regarded as immigrants from outside the Dice's assessment line, their number and relative frequency in the sample being small as follows:

Plot	Female	Male	Total	Frequency rate
A	2	7	13	0.07
B	0	4		

In short, we are naturally led to perceive that a considerable number of immigrants into the census area were induced by the process of capture-recapture trappings. The majority of them, however, have proved to be assigned to the animals with their ranges (strictly speaking, centers of their ranges) inside the assessment line of Dice even before their range shift, the rest referable to the true, effective immigrants (from outside the line) being only a few (7% of the sample).

Herein I ought to call attention to the fact that the ineffective and effective range shifts which occurred at so high rate are by no means ascribed to a peculiarity in the present trapping design, but that, so far as capture-recapture works are concerned, these must have arised, perhaps being induced by allurement of trap-baits to animals, regardless of whether such a process as in this study or a prebaiting or nothing had been performed prior to a proper census trapping. I should say, however, but for a fullfilment of the procedure in the first series, the secret of range shifts could hardly have been disclosed.

How far ranges were shifted by the voles of Types a and b are measured from distances between GCAs before and after a range shift and streches of the post-shift range (Figs. 1~3). Grossly speaking, ranges of immigrants extend on the edge and

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[1] The center of a home range refers to only that of a geometric figure such as circle and ellipse.

nearby trap rows of the census area, but yet to variable degrees some of them reach toward the enter of the area. Accordingly, these immigrants would have caused rather larger catch per trap on the edge and nearby trap rows than at the central area if removal trapping had been worked; then, I should say, the result is an edge effect as a whole. Nevertheless, such an edge effect is seen gradually diminishing toward the center, so that it is almost unlikely that we should find any clear-cut assessment lines demarcating the central area that is utterly free from the edge effect.

PELIKÁN (1969/70), SMITH *et al.* (1969/70), HANSON (1969) and others are researching sampling areas for some assessment lines to escape edge effects in the procedure of density estimation by means of removal trapping. So long as a grid of traps with baits, whether live-traps or snap-traps, are laid out over a census area for an objective population, the same manner of range-shift as Types a and b may be expected to arise as a rule in the light of the present result. As for removal trappings, much immigration may usually be caused by dint of density-vacuum formation within the census area.

Consequently their efforts would be rendered futile eventually ; even if they be successful to detect any assessment lines within plots, they must suffer from the disadvantage, pertaining to their method, that no small number of trapping data taken from outside the assessment lines have to be ruled out from censusing.

There is a research for edge effects based on capture-recapture data but tried by a different analytic means from mine (CHELKOWSKA and RYSZKOWSKI 1967); it reached the conclusions, largely compatible with my above findings, that the true immigrants of the small rodents (*Clethrionomys* and *Apodemus*) did not show so much increase in the number of captures at the edges of the sampling area as expected, and that their captures were evenly spread over the area, whereas, after the complete removal of the rodents from the terrain, an increase in captures at the outer belt, connected with immigration, was clearly visible.

APPROACH TO TRUE SIZE AND SHAPE IN HOME RANGE

As referred to before, I may grant ORL to be a reliable measure for the sake of seeking natural range sizes; thus ORL and ORW were taken of the voles of Type

Table 2. Average lengths (m) of ORL and ORW for the voles of Type c in range-behavior.

Sex	Plot	*n*	Mean no. of capture times	ORL		ORW	
Female	A	23	19.5	20.65±1.43	19.88±1.04	10.96±1.22	9.81±0.79
	B	25	15.0	19.16±1.52		8.76±0.985	
Male	A	18	18.2	32.06±2.98	28.21±1.57	17.06±2.06	15.79±1.13
	B	29	17.9	25.83±1.63		15.00±1.32	

Note: *n* for number of individuals observed.

c which are expected to have revealed range size and shape nearest to the truth. These averages are shown in Table 2.

For neither of these measurements, there is any significant difference between plots; hence both plot values can be combined into single averages, common to both, given to different sexes and measurements respectively. Thus from statistical comparison between these averages it proves to be clear (1) that males are superior to females in either ORL or ORW, and (2) that ORL is nearly twice as long as ORW in either sex.

The first item is nothing but a commonplace knowledge, whereas the second

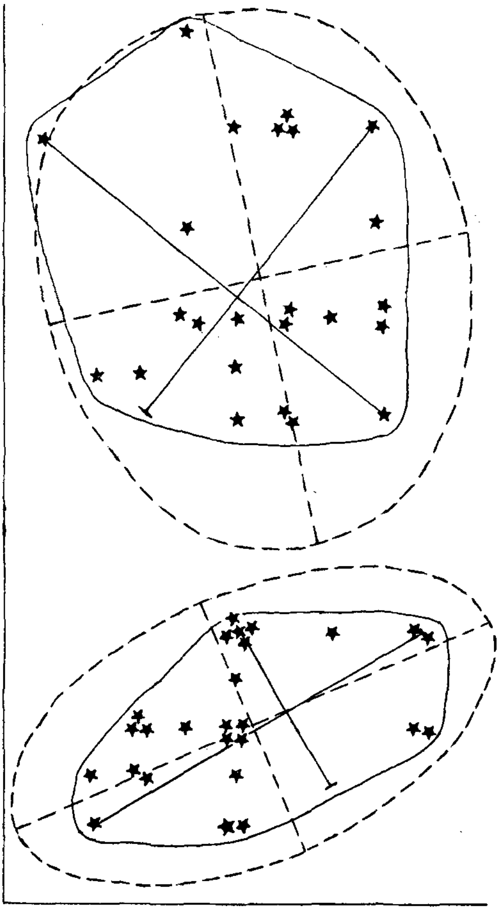

Fig. 4. Solid lines represent home range outline, enclosing an assemblage of capture loci occurred to a single vole (no. of capture times is denoted with no. of pentagrams at each station), and ORL crossed by ORW; dashed lines elliptic outline, accompanied by its long and short axes, (containing 95% of captures) determined by Mazurkiewicz's formulae; abscissa and ordinate show a given set of coordinates axes connected with the trap grid in the study area; examples No. 54 (above) and No. 138 (below), both adult male.

suggests an important notion, the concept of elliptic home range.

To start with, I attempted to calculate elliptical range areas of some examples using MAZURKIEWICZ's formulae which are established on the theoretical ground of bivariate normal distribution, and then these areas were compared with the range sizes as can easily be computed from πab, where $2a$ and $2b$ denote lengths of long and short axes of an ellipse respectively, by putting $2a$=ORL and $2b$=ORW.

In the MAZURKIEWICZ's, a and b on the admission of an ellipse containing 95% of captures are obtained from $a=2.45\delta_u$ and $b=2.45\delta_v$, of which δ_u and δ_v are standard deviations of capture loci under an adjusted system of coordinates. Letting the probability for captures to be contained in a configuration be as much as 95% is granted as right objectively by reference to the usual significance level of 0.05, even though using 95% is obviously of arbitray determination. Unless any arbitrary criterion were imposed, however, the concept of home range would be led to have no fixed outer limit so far as normal bivariate distribution is followed to estimate range size, whether circular or elliptic in shape (TANAKA 1963).

Looking into Fig. 4, bearing in mind the above, we may affirm that the elliptic ranges based on the normal distribution are distinctly larger in area than those determined by use of ORL and ORW and that the latters reveal the truth much better than do the formers in either size or shape. For three examples (adult males), lengths of both axes of elliptic ranges worked out by the two methods at the following (m):

Method		No. 138	No. 239	No. 54
Bivariate normal distribution (95% contained)	$2a$	54	54	56
	$2b$	28	40	46
ORL and ORW	$2a$=ORL	40	36	46
	$2b$=ORW	19	25	39

Previous to MAZURKIEWICZ (1969), every student applied the normal distribution to pooled capture data from different animals so as to be adjusted to circular ranges (TANAKA 1963). TANAKA argued against the methodology in a research into true range sizes for the reasons that: (1) superimposing of data from diverse animals leads us to entertain an unsubstantial range concept, (2) now there is every possibility that a true range has not generally the highest rate of activity frequency at its center, and (3) it has a fixed outer limit about which an abrupt decline in frequency rate of activity seems to occur.

MAZURKIEWICZ succeeded in approaching further the true range shape by remarking the elliptic range concept, but she appears to have missed approaching the true range size by conforming to the normal distribution.

The reliabililty of my method to evaluate the true range size has been demonstrated from some findings with voles of *Microtus* which were deliberately brought forth by the isotope method (GODFREY 1954, AMBROSE 1969). The range shape.

reached by GODFREY also reflected an elliptic trend, but there she did not maintain the elliptic concept as natural range shape.

Their methods of study were very like, but AMBROSE seems to be more advanced than the other in some respects. The larger the distance between the observer and animals, the less the interference of the observer with animals becomes. AMBROSE could detect animals with isotope at a distance of 22 ft (6.7 m), but GODFREY could do so at only 8∼10 ft (2.4 ∼ 3.0 m) distances, from animals. The former obtained as many location finds as 100 or so for a single vole by 3 day tracing, while the latter only 17 ∼ 50 finds by tracing from 10 days to less than 2 months long. As stressed before, it is desirable not to trace too long time for fear any range shift should occur.

Their ways of calculating isotope-revealed range sizes from finds were nearly the same; the range area was determined from the configuration formed by connecting the peripheral location points with right line thereby constructing a polygon with the least possible number of sides passing through these outside finds, and range length and width, each just identical with ORL and ORW, were measured additionally.

GODFREY attempted live-trapping with traps set 6.8 m apart within and without the same area that was studied;as a result she could not find out any evidence that the areas enclosed by the peripheral points, as was located with isotope, underestimated the range size. But AMBROSE discriminated the adjusted range from maximum one that was determined in the way described above; the former, whose outline is composed of some concave lines, looks for us to be much more unnatural and arbitrary than the latter (See Figs. 4 and 6 in his paper). Therefore I would like to adopt only the latter as natural range henceforth.

The matter full of suggestion to us among the contributions by AMBROSE is the comparison, made by superimposition, of trap-revealed ranges induced by diverse means with the isotope-revealed ones. His important conclusions pertinent to me are, in effect, as follows:

The assumption that an animal will range over an area at least one half the distance to the next trap of a grid is not necessarily valid; thereby the exclusive or inclusive boundary strip method founded on the very assumption has proved to cause a gross overestimate of the actual range size in every case of his study, while the minimum area method, which is independent of the assumption and in direct relation to my method using ORL and ORW, has proved to be most accurate.

As for his trapping method, however, it is supposed to have been a positive defect that he took *d* as wide as 50 ft (15.2 m). Such a trap spacing has been ascertained by us (TANAKA 1961, 1962, 1970, TANAKA and KANAMORI 1969, KANAMORI and TANAKA 1968) to be literally too wide for the group of voles to reveal their natural range size. But he was aware of and referred to the defect.

The essential reason why we have adopted ORL as a reliable measure for the real range size instead of "adjusted observed range length" that was recommended by Stickel (1954) as better than ORL from her simulation analysis, is that the above assumption is of no universal validity.

Averages of home range area, range length and width afforded by Ambrose and Godfrey to the voles are shown in Table 3; in addition, for the purpose of comparison, averages of ORL and ORW of my vole (Table 2) and mean range areas calculated from them by the formula πab are exhibited.

Table 3. Calculations of the isotope-revealed range given by Ambrose and Godfrey to *Microtus pennsylvanicus* and *M. agrestis* respectively, accompanied by corresponding values of the trap-revealed range gained in this study.

Authors	Sex	n	Average range area (acres)	Average of range length (=ORL) (m)	Average of range width (=ORW) (m)	Eccentricity c/a
Ambrose (1969)	Female	4	0. 04 }0. 08*	21. 7 }25. 3	12. 5 }16. 5	0. 758
	Male	4	0. 09	27. 4	18. 6	
Godfrey (1954)	Female	22	}0. 048	26. 40±1. 51	15. 34±1. 19	0. 814
	Male	1				
Tanaka	Female	48	0. 04	19. 88±1. 04	9. 81±0. 79	0. 870
	Male	47	0. 09	28. 21±1. 57	15. 79±1. 13	0. 829

* for maximum ranges in his paper.

The table indicates that the calculations in the three studies are corresponding with each other to a surprising degree. The way of area count taken by the isotope-employers was formally different, but hardly so substantially, from mine. The agreement, which can by no means be due to fortuitous coincidence, is remarkable specifically in range area, but also it is grossly acceptable in range shape in terms of ellipse viewed from their eccentricities $(c/a; c=\sqrt{a^2-b^2})$.

In the foregoing papers (Tanaka 1961, 1962), it was claimed that the natural range size of the group of voles is, taken altogether, of the order of 25~30 m in length (ORL) of their home range at ordinary density levels. Thus the present results in Table 3 are obviously in support of the claim, except that ORL was rather large for the density (60 or so per acre) given to this vole population. The range size, however, was calculated exclusively on the unlikely assumption that a home range is universally circular at the time of these studies, so that, supposing the range diameter to be ORL, the range area was overestimated at as much as 0. 13 acres against ORL=25. 6 m.

On the ground of the findings and the above discussions, I could be assured that, on the average, the true home range of the vole population was probably 0. 04 for females and 0. 09 for males in acreage and that it was elliptic outline such as its eccentricity is 0. 76~0. 87.

THEORETICAL ANALYSIS OF EDGE EFFECT

A trapping quadrat (side length l) formed of a grid system at intervals of d can be reflected by several concentric squares of trap rows as in Fig. 5.

Provided that DICE's assessment line is h distant from the outermost trap row (1), his notion to calculate the density (D) is expressed as follows:

$$D=\hat{N}/(l^2+4\,hl+\pi h^2)$$

$$\text{or} \qquad \fallingdotseq \hat{N}/(l^2+4\,hl) \qquad \text{when } l \gg h \qquad (1)$$

where $\hat{N}$ is the population estimated by sampling from the quadrat ABCD, and $h=1/2\sqrt{H}$ letting H be a mean acreage of home range. The theory was built up on the supposition that the animals, whose centers of home range (assumed as circle) are distributed within the width h, may be contained in the sample.

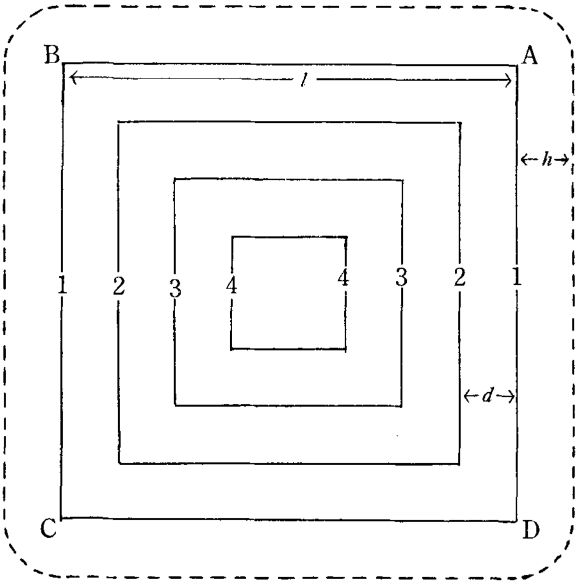

Fig. 5. Illustrating concentric trap-row squares of which a grid system of trap-stations, spaced d apart, is composed, and an additional boundary strip, h in width, demarcated by DICE's assessment line (dashed line); quadrat ABCD (side length l) shows the trapping area marked with trap-rows (1), (2), (3),⋯⋯.

Thus far, however, I have mentioned of the methodological difficulty in obtaining directly the true range size in terms of acreage. But, instead, I have come to follow the way of measuring ORL or both ORL and ORW as a feasible means through which to attain the true size.

Under the circumstances, I should prefer to adopt $h=1/2$ ORL on the premise of circular range and $h=1/4$ (ORL+ORW) on that of elliptic range rather than obey DICE's rule above stated. Then, from our present data, based on elliptic ranges, chiefly of adult voles, the general mean of h was given at 9.2 m from Table 2.

On the other hand, the intra-plot assessment line was detected by discriminating the inner square having homogeneously lower values in catch per trap from the outer belt having higher ones (PELIKAN, SMITH *et al.*, HANSON). But, among them, HANSON (1969) used h such as computed from the following equation, based on Eq. (1), to distinguish the effect of invasion among the gross edge effect:

$$\hat{N}_b/b^2=\hat{N}_a/(a^2+4\,ah+\pi h^2) \qquad (2)$$

where $\hat{N}_a$ is a population estimate from the quadrat (ABCD in Fig. 5) and $\hat{N}_b$ that from the inner square homogeneous in catch per trap, a and b being several side lengths. The left side of Eq. (2), however, would seem to be unjust, for we should allow for the edge effect on the inner square as well as on the whole quadrat.

Anyhow, HANSON thinks outright that such edge effect as expressed by increased catch per trap, may result both from residents on the adjoining area outside a quadrat and from immigrants. In the case quite free from the effect of immigration, it looks needful for us to analyse, from theoretical standpoint, whether or not the former agent will help to yield the edge effect.

Let each animal of a population (N) have a circular home range with mean radius (h) and each center of range be distributed at random on the whole area, enclosed with DICE's assessment line (dashed line in Fig. 5), which involves the trapping quadrat (ABCD) and the additional boundary strip. Since the diameter of a range is regarded as ORL, we get $h=1/2$ ORL. And then, viewed from location of centers of home ranges, N is to be divided into N_E, distributed on the belt terrain circumscribed by the dashed line and trap-row (2), and N_I, situated inside the trap row (2), and it is proved from Fig. 5 that $N\fallingdotseq(l+2h)^2\delta$ and $N_E\fallingdotseq4(l-d+h)\ (d+h)\delta$, δ standing for population density.

Herein, for brevity's sake, I would like to consider the special case of $d=h$. Then the following are obtained:

$$N=(l+2h)^2\delta,\ \ N_E=8lh\delta \text{ and } N_I=(l-2h)^2\delta \qquad (3)$$

Of the two groups of N, individual ranges of N_E are supposed to touch sides of ABCD, i. e. trap-row (1), at a point at least, while any individual ranges of N_I never touch the trap row (1), no contact of an animal's range with a trap row implying that the animal is unexposed to any trap on the row.

According to MORISITA and MURAKAMI (1968), under the aforesaid conditions, the mean area of the portion of home ranges, that is located within the quadrat ABCD, of the above population (N) is approximately given by the following:

$$E(S)\fallingdotseq\pi h^2\{l/(l+2h)\}^2 \qquad \text{when } l\geq2h$$

Therefore, supposing $E(S')$ to be the corresponding mean area for the group N_E, we get

$$N\pi h^2\{l/(l+2h)\}^2=N_I\pi h^2+N_E E(S'). \qquad (4)$$

By substituting Eqs. (3) into (4), we get

$$E(S')=\pi h^2(l-h)/2l.$$

Then, on the likely presumption that the catchability for each animal in a given trapping period is proportional to area of the portion of respective home ranges that is located within the trapping quadrat (ABCD), the total catches (C_E, C_I) out of the N_E and N_I groups are expected to be as follows:

$$C_E = k.\ (\pi h^2(l-h)/2l).\ 8\,lh\delta = 4\,k\pi h^3(l-h)\delta/l$$

$$C_I = k.\ \pi h^2.\ (l-2\,h)^2\delta$$

where k is a constant for catchability.

The majority of C_E are captured in the outermost trap row (1) (all sides of ABCD), but the rest may be done either in trap-row (2) or in (3). Supposing that all of C_E were captured in trap-row (1), the catch per trap ($C_E{}^*$) is calculated as subsequently:

$$C_E{}^* = 4k\pi h^3(l-h)\delta/l \div 4l/h = k\pi h^4(l-h)\delta/l \qquad (5)$$

As for N_I group, each animal can be exposed to every trap row except (1), so that

$$C_I{}^* = k\pi h^2(l-2h)^2\delta/\{(l-2h)/h+1\}^2 = k\pi h^4(l-2h)^2\delta/(l-h)^2. \qquad (6)$$

By the above reason we see that Eq. (5) shows a maximum estimate of real values of $C_E{}^*$, but that Eq. (6) denotes a minimum estimate of real values of $C_I{}^*$.

In fact, the catches per trap on the external belt and on the inner square are usually compared in order to check up the edge effect, and hence the ratio $\rho = C_E{}^*/C_I{}^*$ has been inquired into. From Eqs. (5) and (6), we obtain

$$\rho = (l-h)^3/l(l-2h)^2.$$

In general, ρ is over unity, but it approximates unity when $l \gg h$; for instance, if $l=3h$, $10\,h$ or $100\,h$, $\rho = 2.67$, 1.14 or 1.01 respectively. Therefore, also by reference to the real values of $C_E{}^*$ and $C_I{}^*$, it is very likely that ρ is nearly unity. Seeing that the theoretical justification is not yet generally established, I may tentatively

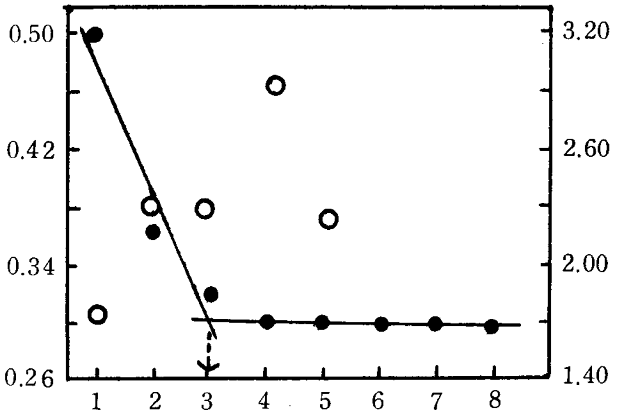

Fig. 6. Determination of the intra-plot assessment line by Smith et al. (1969/70); solid dots indicate their catches per trap on each of trap-rows 1 to 8 (abscissa) such as illustrated in Fig. 5, the intersection of both fitted lines locating the assessment line. Our catches per trap (cited from Tanaka and Kanamori 1969) are plotted on the corresponding trap rows respectively, the figures on the right ordinate standing for our catches.

say that there can be no edge effect such as revealed by increased catches per trap unless any immigration onto the sampling quadrat occurs.

The intra-plot assessment line was guessed by SMITH *et al.* from the detected intersection of both lines fitting stable catches in inner trap rows and higher catches in outer rows (Fig. 6). In spite of their remark, these catch data, strictly speaking, are suggestive of a curvilinear arrangement, leading to equivocal location of the assessment line. Moreover, the notable superiority in catches of the outer two rows over the inner rows expresses obviously the proof for intense invasion according to the above demonstration, whereas the authors claimed that invasion hardly arised, from their judgement of other data.

Our catch data, taken in 1969, exhibited in the same way as in their paper (Fig. 6) have produced rather a reverse relation to their result; from the relation it follows that anything like invasion scarcely occurred to the then population, and that we cannot always expect homogeneous catches from row to row of trap even when no invasion is confirmed.

POPULATION PARAMETERS

Parameter-estimation of the vole population during the study period has been attempted. The two sampling plots (A, B) were provided with very like populations and habitats except for some difference in density between them, and then the samples each alone were not always sufficient for statistical analysis. Thus the capture records from both plots were combined for computation of parameters (Table 4).

Of the three series of sampling, Ser. (1) was conducted on the whole area (Figs. 1~3) in either plot, but both Sers. (2) and (3) were in common founded on the inner square (the proper census area) only, so that the catches adjusted for parameter-count ought to have been separated into the two chains of samplings, made at given intervals, the first for Ser. (1) being called "prior chain" and the second for Sers. (2) and (3) called "proper chain". MC and EC on the column of date in Table 4 refer to the morning and the evening check respectively.

The notation for variables and parameters in the table are interpreted as subsequently. Herein it is worthy of note that capture-recapture works had been executed at successive intervals on the plot area before the setout of the present study, with the result that a number of marked animals, which had been captured for the first time from 1 to 12 months previous to the start, were recaptured in both prior and proper chains, hence such recaptures having been discriminated from the quite new animals (U_i).

U_i: number of new captures, at time i, that had never been caught before the prior chain was started and also before time i of each chain.

R_i: number of recaptures, at time i, which had been caught for the first time previous to the respective setouts (Aug. 8 and Aug. 12) of the prior and the proper chain.

Table 4. Capture records and estimates of population parameters from the pooled data of both plots (A, B); see text as to explanations.

Series	Date (Aug. 1970)		Time (i)	U_i	R_i	m_i	$\hat{\Psi}_i$	$\hat{P}_i$	$\hat{\pi}_i$ ($m_i/\hat{\Psi}_i$)
(1)	I (8)	MC	1	49(1)*	90	0	0	0.979±0.009	—
		EC	2	14	9	81	135.04±1.27	0.993±0.013	0.600
	II (9)	MC	3	23	10	117	156.86±1.58	0.969±0.015	0.746
		EC	4	4	3	90	183.90±2.43	0.997±0.015	0.489
	III (10)	MC	5	19	3	138(1)*	190.26±2.78	0.964±0.027	0.725
		EC	6	7	1	125	203.59±5.11	0.926±0.040	0.614
	IV (11)	MC	7	16(1)*	2	150	195.88±6.99	—	0.766
		EC	8	2	1	116(1)*	—	—	—
	Total			134	119				
(2)	V (12)	MC	1	0	83	0	0	0.998±0.014	—
		EC	2	1	22	51	82.86±1.13	0.981±0.015	0.615
	VI (13)	MC	3	3	23	64	103.89±1.15	0.996±0.018	0.616
		EC	4	0	7	70	129.31±2.06	0.970±0.018	0.541
	VII (14)	MC	5	2	6	78	132.26±1.45	1.000±0.020	0.590
		EC	6	0	6	75	140.22±2.46	0.955±0.018	0.535
	VIII (15)	MC	7	1	4	80	139.70±1.08	0.996±0.012	0.573
		EC	8	2	3	67	144.07±1.50	0.987±0.010	0.465
(3)	IX (16)	MC	9	16	19	136	147.13±0.37	0.996±0.008	0.924
		EC	10	2	1	134	181.38±1.38	0.975±0.009	0.739
	X (17)	MC	11	9	3	160	179.81±0.98	0.968±0.009**	0.890
		EC	12	0	2	131	185.64±1.54	0.987±0.012	0.706
	XI (18)	MC	13	16	8	163	185.26±1.67	0.917±0.014**	0.880
		EC	14	2	0	129	191.84±2.47	0.966±0.020	0.672
	XII (19)	MC	15	9	4	172	187.29±2.96	—	0.918
		EC	16	2	0	131	—	—	—
	Total			65					

* one animal dead in captivity in the group.
** showing clear difference from unity.

m_i: number of the marked animals, which were handled during the period from time 1 to $i-1$ of each chain irrespective of whether they had ever been caught or not before Aug. 8, in the ith sample.

$\hat{\Psi}_i$: estimated total number of the marked animals in the population at time i ($i=2, 3, \ldots\ldots T-1$),

$\hat{P}_i$: estimated probability that one of the marked animals alive and released at time i will survive till the time of capture in the $i+1$ th sample ($i=1, 2, \ldots\ldots, T-2$).

$\hat{\pi}_i$: estimated probability that one of the marked animals alive at time i will be caught in the ith sample.

The last three parameters were estimated through JOLLY's formulae (1965) with the most universal validity to capture-recapture data except that the estimate $\hat{\pi}_i$ was given by $m_i/\hat{\Psi}_i$; thus I could not be afforded any facilities to find a variance-formula for $\hat{\pi}_i$ to my sorry. But the estimate is accoundted as much more trustworthy than that which used to work out in my foregoing papers only from m_i/M_i (M_i for cummulative sum previously captured and released).

From $\hat{\pi}_i$-values in Table 4 and Fig. 7, it is readily recognized that: (a) they are distinctly larger in Ser. (3) than in Ser. (2), the discrepancy being doubtless due to greater trap density, viz. closer trap spacing, in that than in this; (b) they indicate consistently some or marked difference between the morning and the evening check assigned to each day, the distinction being referable to a longer time of trap-exposure and/or a higher amount of activity in animals at night than in the daytime, even if we are awared of a noticeable daytime activity of the vole; (c) they are, respectively in each of the four groups of MC and EC in both series, kept nearly the same but suggestive of rather declining towards the end, the trend being inexplicable but serving to disprove that any increased times of capture never cause a raised value of π for an individual.

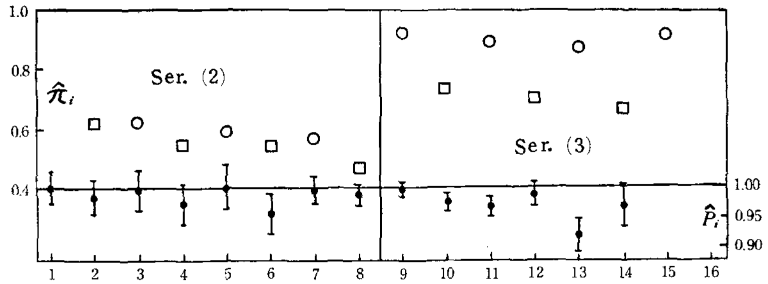

Fig. 7. Above: showing time to time change in estimate of probability of capture ($\hat{\pi}_i$) for marked animals at the successive sampling times (i, abscissa) of the proper chain; circles for MC, squares for EC. Below: survival probability ($\hat{P}_i$) for the marked animals at the same sampling times, the estimates with 95% confience intervals being denoted.

In view of the survival probabilities with confidence intervals in Fig. 7, every value cannot be clearly distinguished from unity except for two cases $i=11$ and 13 in Ser. (3), despite the fact that the difference of $\hat{\Psi}_i$ from M_i amounted to as much as to be fully significant in many cases of later times. At any rate, attaching importance to the fact that only two cases ($i=11$ and 13) possessed $\hat{P}_i$ quite significantly lesser than unity, the overall rate of emigration will be guessed at 0.11 from $\hat{P}_{11}\times\hat{P}_{13}=0.89$, for the survival rate lesser than unity may justly be accounted for mostly by emigration of marked animals out of the proper quadrat so far as this work is concerned.

In the foregoing section, I pointed out that about 7% of the population must have made effective immigration onto the quadrat in the course of proper sampling. Presumably the emigration rate (11%) is a value compensating for the immigration rate (7%); hence I might suppose that the population was retained almost invariable during the period of this work.

Next, I should proceed to estimating population N and probability of capture (p) for unmarked (new) animals belonging to U_i group. As for our voles and the like, it is an indisputable fact[1] that π_i is nearly always superior to p_i, even if the population underwent prebaiting previous to a census sampling (TANAKA 1956, 1970, KANAMORI and TANAKA 1968). Under such circumstances, the excellent method of JOLLY (1965) becomes unavoidably invalidated so far as the estimation of N and p is concerned.

Accordingly I had to follow the regression census method expressed in terms of the basic formula,

$$C_n = (N - S_{n-1})p \qquad (7)$$

By use of this equation, we can esimate the initial size (N) of U_i group or of R_i group only if we deal with catches (C_i) in the ith sample paying attention to out of which group they were taken (Fig. 8).

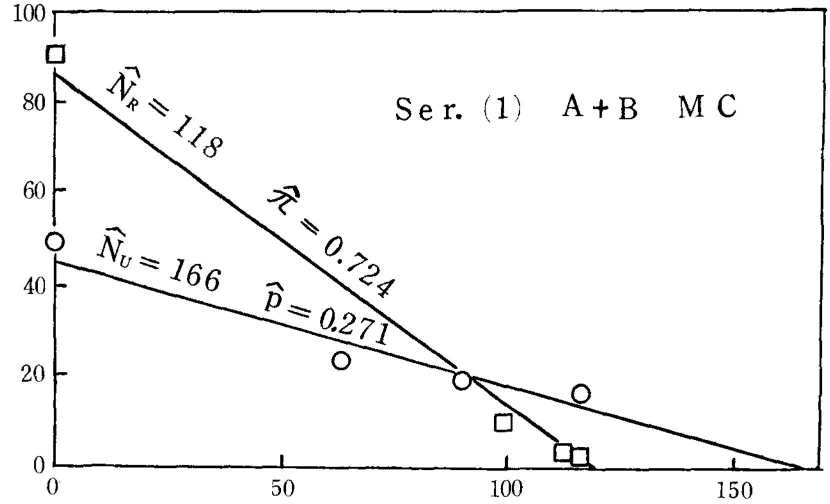

Fig. 8. Affording maximum likelihood estimates for respective population sizes of the U_i and the R_i group and for probability of capture pertaining to each group by following Eq. (7); C_n from N_R or N_U is on the ordinate and S_{n-1} on the abscissa, based on combined MC data of both plots in Ser. (1).

In applying the equation to a set of catches in several chains of sampling, we need to adopt either the data of MC only or of EC only, or to take the combined data of MC and EC assigned to each day by reason of the item (b) above mentioned. For the justification of the last case, it can be verified that the constant catch rate (let it be p^*), to be used instead of p in Eq. (7), is represented as follows:

$$p^* = p_{MO} + q_{MO}\, p_{EO} \qquad (8)$$

where $p_{MO} \fallingdotseq p_{EO}$ and $q_{MO} = 1 - p_{MO}$ (unpublished).

Further, the same probability of capture cannot be expected through the course of proper chain because of the distinct alteration in d from Ser. (2) to (3).

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[1] Refer to MARTEN (1970) and SEVER (1970) as to the latest consideration of capture-recapture censusing in the case of $\pi \fallingdotseq p$.

Owning to the restricted availability, the capture records in Table 4 are not quite enough for censusing. Then I could calculate only two maximum likelihood estimates ($\hat{N}_U$ and $\hat{N}_R$) of sizes of the U_i and the R_i group at the initial time ($i=1$) of the prior chain, viz. Ser. (1), by following Eq. (7) applied to the data of MC only[1] (Fig. 8). The estimates for them and for probability of capture pertaining to them, thus obtained, were as follows:

$$\begin{cases} \hat{N}_U = 166 \pm 7.86 \\ \hat{p}_{MO} = 0.271 \pm 0.0575 \end{cases} \qquad \begin{cases} \hat{N}_R = 118 \\ \hat{\pi}_{MO} = 0.724 \end{cases}$$

The probability of capture pertaining to N_U should be denoted with letter p_{MO}, which is involved in Eq. (8), its subscript representing that it was assessed on the basis of MC data only, while that pertaining to N_R should be marked with letter π because the R_i group in Ser. (1) is represented by the animals which had been caught one month or more before the initial day of the series. As has been anticipated, the given value for π_{MO} agreed well with those for $\hat{\pi}_i$ of MC in Ser. (1), whereas the value of $\hat{p}$ pertaining to U_i is so much smaller than any of the $\hat{\pi}_i$-values in Table 4, that significant difference must have been established.

Summing up, these findings show that the vole population also is plainly of $\pi > p$ type in trap-response, and that the trap-experience, which animals underwent one month or more ago, can make them retain such high catchability as characteristic of marked captures among the sample in a series of census trappings.

As a consequence of the above census, the initial total population on the whole area (EB+IS) of both plots combined in the prior chain was estimated at 284 as $\hat{N}_U + \hat{N}_R$; it leads to $D_W = 41.5$ per acre under the theory of DICE's assessment line, putting $h = 9$ m as a result of this range study.

On the other hand, so far as the proper chain is concerned, I hesitated in censusing the U_i group from the catch data, but it seems very likely that something of the $\hat{\Psi}$-values near the end of the last series approximates the overall population level in the proper chain, seeing that only a few or none of the U_i or the R_i group were captured at the end. Thus I have reasonably adopted $\hat{\Psi} \fallingdotseq 190$, with the result that $D_I = 64.0$ per acre is given to the inner square.

The appreciable increase of D_I over D_W would be accounted for mostly by the fact that D_W was possibly some underestimate due to trap-unexposure, on the part of animals, caused by wider trap-spacing (10 m); quite different as the census method was between both densities, D_I ensued from sampling on the 5 m-spaced grid in Ser. (3) at least (TANAKA 1970). Immigration which occurred in the proper chain might be partly responsible for the discrepancy in density estimate, but the interpretation would be negligible, since I could recognize that the immigration and emigration were roughly correspondent with each other in rate during the study period.

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[1] In this case, we have to follow SUGIYAMA's method to obtain maximum likelihood estimates (refer to TANAKA 1956).

SUMMARY

A substantial explication of the edge effect has been attempted by use of capture-recapture data for a vole population (*Microtus montebelli*), gathered in two plots of 100×100 m or less during 12 days, cheked twice daily, in August 1970; the sample was quite sufficient for the aim.

The edge effect as guessed by increased catch per trap is usually suspected to ensue from range-settlers in the outside boundary strip of a plot and immigrants. But by a theoretical analysis I could attain a tentative conclusion that no increased catch per trap will occur unless any invasion takes place. Then it follows that, apart from the effect of invasion, the role of the adjoining outside settlers in the edge effect is essentially required to be studied in the light of knowledge on the truth of size and shift in home range.

The variation in range behavior for 183 adult voles, captured 6 times or more, could be grouped into eight types, of which the range-conservative type possessed 52% of the sample and the group of the type was justly utilized for giving averages of range size. Besides, it was seen from the observed frequency of types that a considerable number of immigrants onto the census plot were induced perhaps being allured by trap baits, but the majority of them proved to be assigned to the voles that have their ranges inside the assessment line of DICE; the rest referable to effective immigrants was only a few (7%). I could perceive no reason such as disproves the idea of DICE's additional boundary strip.

Viewed from maps of ingress shift of ranges, the effect of ingress must have been greater in the outer trap rows than in the inner within the plot, so that it might well be called edge effect in general; such effect, however, is seen gradually diminishing toward the center, and hence it is almost unlikely that one should find any clear-cut intra-plot assessment lines demarcating such an inner square as quite free from edge effects.

Averages of observed range length and width (ORL and ORW), as reliable measures for the true range size, were determined from the above group of specimens; as a result, the remarkable concept of elliptic range shape was established by regarding ORL as long axis and ORW as short one, and, directly from these averages, the mean range sizes worked out at 0.04 for females and 0.09 for males in acreage which proved to be surprisingly well agreeable with those of isotope-revealed ranges for voles given by GODFREY (1954) and AMBROSE (1969).

The catchability for marked voles ($\hat{\pi}$) was estimated by the maximum likelihood method by use of JOLLY's formulae (1965), but that for unmarked ones ($\hat{p}$) was made by the regression census formula; as a result it was shown that the population was clearly of $\pi > p$ type and that the trap-experience that voles underwent one month or more ago can make them retain as high catchability as π.

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References

Ambrose, H. W. III (1969) A comparison of *Microtus pennsylvanicus* home range as determined by isotope and live trap methods. *Amer. Midl. Nat.* 81 : 535-555.

Burt, W. H. (1943) Territoriality and home range concepts as applied to mammals. *J. Mamm.* **24** : 346-352.

Chelkowska, H. and L. Ryszkowski (1967) Causes of higher abundance estimates of small rodents at the edges of sampling area in forest ecosystems. *Ekol. pol. A* **15** : 737-746.

Dice, L. R. (1938) Some census methods for mammals. *J. Wildl. Mgt.* **2** : 119-120.

Godfrey, G. K. (1954) Tracing field voles (*Microtus agrestis*) with a Geiger-Muller counter. *Ecology* **35** : 5-10.

Hanson, L. (1969) Home range, population structure and density estimate at removal catches with edge effect. *Acta theriol.* **14** : 153-160.

Jolly, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52** : 225-247.

Kanamori, M. and R. Tanaka (1968) Studies on population ecology of the vole, *Mirotus montebelli,* in mountain grassland of Sugadaira and its adjacent areas, I Results of research on five populations in 1966-1967. *Bull. Sugadaira Biol. Lab., Tokyo Kyoiku Univ. No.* **2** : 17-39. (in Japanese with English summary)

Marten, G. G. (1970) A regression method for mark-recapture estimation of population size with unequal catchability. *Sm. Mamm. Newslet.* 4 : 31-44.

Mazurkiewicz, M. (1969) Elliptical modification of the home range pattern. *Bull. Acad. Pol. Sci. Cl. II,* **17** : 427-431.

Mazurkiewicz, M. (1971) Shape, size and distribution of home ranges of *Clethrionomys glareolus. Acta theriol.* **16** : 23-60.

Mohr, O. (1965) Calculation of area of animal activity by use of median axes and centers in scatter diagrams. *Res. Pop. Ecol.* 7 : 73-86.

Morisita, M. and O. Murakami (1968) Methods to estimate home range sizes in small mammals. Lecture at 15th *Ann. Meet. Ecol. Soc. Japan.*

Pelikán, J. (1969/70) Testing and elimination of the edge effect in trapping small mammals. *Proc. IBP Meet. Sec. Prod. Sm. Mamm. Pop. Oxford,* pp. 57-61.

Sever, G. A. F. (1970) The effects of trap response on tag recapture estimates. *Biometrics* **26** : 13-22.

Smith, M. H., J. B. Gentry and F. B. Golley (1969/70) A preliminary report on the examination of small mammal census methods. *Proc. IBP Meet. Sec. Prod. Sm. Mamm. Pop. Oxford,* pp. 25-29.

Stickel, L. F. (1954) A comparison of certain methods of measuring ranges of small mammals. *J. Mamm.* **35** : 1-15.

Stickel, L. F. and Warbach (1960) Small mammal populations of a Maryland woodlot, 1949-1954. *Ecology* **41** : 269-286.

Tanaka, R. (1956) On differential response to live traps of marked and unmarked small mammals.

Annot. Zool. Jap. **29** : 44-51.

TANAKA, R. (1961) A field study of effect of trap spacing upon esimates of ranges and populations in small mammals by means of a Latin square arrangement of quadrats. *Bull. Kochi Wom. Univ. Ser. Nat. Sci.* **9** : 8-16.

TANAKA, R. (1962) A population ecology of rodent hosts of the scrub-typhus vector of Shikoku district with special reference to their true range in Japan. *Jap. J. Zool.* **13** : 395-406.

TANAKA, R. (1963) Truthfulness of the delimited-area concept of home range in small mammals. *Bull. Kochi Wom. Univ. Ser. Nat. Sci.* **11** : 6-11.

TANAKA, R. (1970) A field study of the effect of prebaiting on censusing by the capture-recapture method in a vole population. *Res. Pop. Ecol.* **12** : 111-125.

TANAKA, R. and M. KANAMORI (1969) Inquiry into effects of prebaiting on removal census in a vole population. *Res. Popul. Ecol.* **11** : 1-13.

ハタネズミ個体群における記号法データによる周辺効果の検討

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IBP 研究の進展につれて，開放系調査区からとったネズミ個体群のセンサスデータから推定した個体数から密度の実体を導くために，周辺効果をどう処理するか，ということが問題になってきた。

わたくしは，1970年8月菅平草原の本種個体群から記号法データをとり，主にホームレンジの保持・転位に着目して，周辺効果の実体論的解析を試みた。その結果，餌を付したわな（生捕または捕殺用であれ）の格子型配列系によるサンプリング自体が意外に多い侵入者（レンジ転入者）の数（52%）を招く恐れがあることがわかったが，しかし，そのうち DICE (1938) の密度査定線の外側からの侵入者（実効的侵入者）数はごくわずか（7%）であるとみなされた。実体的ホームレンジの大きさをつかみえれば，DICE の査定線は有用であり，それに対して，最近若干の学者が追求している調査区内査定線は非実体的なもので，また，それが見出されたとしても非実用的である。なお，この個体群のホームレンジの実体は，平均0.04（雌），0.09（雄）エーカーの大きさで，離心率0.8位の楕円形を示すことが認められた。